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Host-specific demography of *Utetes anastrephae* (Hymenoptera, Braconidae), a native parasitoid of *Anastrepha* spp. fruit flies (Diptera, Tephritidae)

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Abstract

The braconid *Utetes anastrephae* (Viereck, 1913) (Hymenoptera: Braconidae) is a larva-pupal parasitoid of fruit flies of the genus *Anastrepha* Schiner, commonly associated with *Anastrepha obliqua* (Macquart, 1835) (Diptera: Tephritidae), the most important pest of mango (*Mangifera indica* L., 1753) in Mexico. This parasitoid was established in a laboratory colony using larvae of *Anastrepha ludens* (Loew, 1873) as host. Here we describe a demographic study to compare the reproductive and population parameters of this parasitoid reared on *A. obliqua* and *A. ludens* under laboratory conditions. Two *U. anastrephae* cohorts of 30 individual pairs each were set up, one was reared on *A. obliqua* larvae and the other one on *A. ludens*. Every day, 30 third instar larvae of each host species were exposed to an adult pair through the lifespan of the female. Daily mortality and fecundity were recorded. Life tables were constructed and sex ratios, parasitism rates, survival, reproductive and population parameters were estimated. Higher survival of *U. anastrephae* females was observed in females from *A. obliqua* (mean live expectancy of 22.4 days), but higher fecundity and parasitism occurred in females from *A. ludens* (net fecundity of 62.61 daughters/female and 16.72% parasitism rate). The intrinsic rate of increase ($r = 0.128$ and $r = 0.134$ for *A. obliqua* and *A. ludens* respectively), mean generation time (27.88 and 28.30 days) and population doubling time (5.42 and 5.16 days) were similar in both cohorts, as well as the sex ratio (73 and 69% of females). These results suggest that *A. ludens* as host increase the production rates; however, any one of these two species could be used as host for mass rearing purposes.

Keywords

biocontrol, fecundity, intrinsic rate of increase, life table, mass rearing, parasitism, survival

Introduction

The use of native parasitoids for the management of *Anastrepha* fruit flies has been a subject of discussion, since these species would be used in an environment where fruit flies generally have a higher rate of natural increase (Vargas et al. 2002; Aluja et al. 2009). However, given the good results obtained with augmentative releases of *Diachasmimorpha longicaudata* (Ashmead, 1905) in different environments (e.g., Montoya et al. 2000; Montoya et al. 2007; Montoya et al. 2016; Cancino et al. 2019a), the potential for native species for the control of *Anastrepha* fruit flies is worth to explore.

Utetes anastrephae (Viereck, 1913) (Hymenoptera: Braconidae) is a koinobiont, solitary endoparasitoid (Ovruski et al. 2000) native to the Neotropics that parasitizes larva-pupa of fruit flies. It is found parasitizing *Anastrepha obliqua* (Macquart, 1835) (Diptera: Tephritidae) feeding upon *Spondias* spp. (Anacardiaceae), and in minor frequency in other species such as *Anastrepha alveata* Stone, 1942 and *Anastrepha fraterculus* (Wiedemann, 1830) (Aluja et al. 1990; Hernández-Ortíz et al. 1994; López et al. 1999). This parasitoid competes successfully with other native braconid parasitoid species, such as *Doryctobracon areolatus* (Szépligeti, 1911), *Doryctobracon crawfordi* (Viereck, 1911), and *Opius hirtus* Fischer, 1963; it even competes with the introduced *D. longicaudata*, showing a remarkable capacity for conspecific discrimination and heterospecific intrinsic competition in previously parasitized larvae (Aluja et al. 2013; Ayala et al. 2018; Murillo et al. 2018).

The use of a parasitoid species for augmentative biological control applications requires the development of methods for mass production of good quality individuals. One essential element is the selection of an adequate host species (Eitam et al. 2003; Cancino et al. 2009). Although *A. ludens* is not considered a preferred host for *U. anastrephae*, it can be used as an alternative host because it is a species relatively easy to rear, being a high-quality host that is currently used to produce massively *D. longicaudata* (Orozco-Dávila et al. 2017; Cancino et al. 2020). Under laboratory conditions *U. anastrephae* successfully parasitizes 5–8 days old *A. obliqua* larvae (Poncio et al. 2018) and 7–8 days old *A. ludens* larvae (Aluja et al. 2009; Cancino et al. 2009).

Knowledge of the demography of parasitoids, in addition to allowing a better understanding of their biology, allows us to compare the effect of different hosts and make mass rearing more efficient (Bellows et al. 1992; Carey and Roach 2020; Ganjisaffar and Perring 2020). For example, the intrinsic rate of natural increase (r) is a population parameter described as the potential growth of a population (Jervis and Copland 1996) and can be used as an indicator of the capacity of a parasitoid species to suppress or regulate the target pest population (Vargas et al. 2002; Stark et al. 2004). This parameter combines both the survival and reproduction of a population and allows

comparison among different species of parasitoids or when species are evaluated under different environmental conditions (Núñez-Campero et al. 2014; Gonçalves et al. 2018; Fernandes et al. 2021).

Our previous trials, trying to establish a colony of *U. anastrephae* using *A. obliqua* larvae as host, were unsuccessful, despite being considered its natural host. Here, we used a strain of *U. anastrephae* reared on *A. ludens* larvae as host, applying the concept of factitious host used for *Trichogramma* spp. mass rearing (Iranipour et al. 2010; Gowda et al. 2021). Our hypothesis was that the demographic parameters of *U. anastrephae* would be affected by the host species used for the development of their offspring. Therefore, our aim was to determine the effect of two different hosts, *A. obliqua* (the preferred host in nature) and *A. ludens* (the host used in laboratory rearing), on the survival, reproductive and population parameters of *U. anastrephae*. Our results improved our understanding of the performance of *U. anastrephae* reared on both host species and indicate that both can be used for mass rearing it as a biocontrol agent of *Anastrepha* fruit flies.

Materials and methods

Biological material

The study was carried out at the Laboratory of Biological Control, of the Programa Moscafrut (SENASICA-SADER) in Metapa de Domínguez, Chiapas, Mexico. *Utetes anastrephae* specimens were obtained from a laboratory colony maintained using *A. ludens* larvae as hosts. This colony was established with specimens of *U. anastrephae* emerged from larvae of *A. obliqua* developed in tropical plum trees (*Spondias mombin* L.). After three unsuccessful attempts using *A. obliqua* as host, we decided to use *A. ludens* as alternative host. This strategy was successful in terms of colonization and the current colony has ≈ 250 generations under laboratory mass rearing conditions. The larvae of both *A. ludens* and *A. obliqua* were obtained from the mass reared colonies maintained at the Moscafrut facility (Orozco-Dávila et al. 2017). All experiments were carried out under laboratory conditions at 26 ± 0.5 °C, $70 \pm 10\%$ relative humidity, and a 12:12 h L:D photoperiod.

Oviposition period, parasitism rate and adults sex ratio using two species of host larvae

Two cohorts of *U. anastrephae* of 30 pairs (♀ , ♂) each were set up. Individual pairs of newly emerged adults were placed in $25 \times 11 \times 13$ cm plastic cages. They were provided with water and honey throughout the experiment. One cohort was exposed to *A. obliqua* and the other one to *A. ludens*. Each pair was daily provided with 30 larvae of the corresponding species along the lifespan of each female. The larvae were exposed in parasitization units consisting in 5 cm diameter \times 0.2 cm height Petri dish bottoms,

mixed with larval diet, and covered with tricot fabric clothe fastened with an elastic band. The surface of the parasitizing unit was smeared with ripe guava pulp to attract the parasitoids.

Parasitization units were exposed 4 h every day. Then the larvae with diet were placed in 6 cm diameter × 4 cm height plastic containers. Three days later the larvae were carefully sorted out from the diet with entomological forceps and returned to the same container but now with humid vermiculite as a pupation substrate. The pupae were maintained in humid vermiculite for 14 days at 26 ± 0.5 °C and 60–80% RH. Subsequently, the pupae were removed from the vermiculite and kept in these same conditions until emergence.

The number of dead parasitoids and their sex was recorded daily to estimate sex-specific survival. The number of flies and parasitoids emerged by sex were also recorded every day. Pupae that did not emerge were dissected to investigate the presence of parasitoids or flies. The oviposition period was determined based on the emergence of parasitoids per day. The percentage of parasitism was obtained by dividing the number of emerged parasitoids by the number of exposed larvae, multiplied by 100, as well as the percentage of accumulated parasitism (daily sum of parasitism). The sex ratio of the parasitoids was estimated by dividing the number of females by the sum of females and males and was expressed as the proportion of females.

Life tables and reproductive and population demographic parameters

To know the survival of the immature stages, 400 larvae of each host species were exposed to two separate groups of 30 couples of five-day old *U. anastrephae* adults; from each host species 20 subsamples of 20 larvae were obtained, and each subsample was dissected daily to know the number of immatures. For life table construction we used the mean egg to adult developmental time and percent survival for each host species.

With the mortality and fecundity data, the corresponding life tables were elaborated, following methods described by Carey (1993), and Carey and Roach (2020). Survival curves were estimated with the proportion of live females per day (I_x), that is the number of live females at age x between the original number of the cohort ($I_0 = N_0 / N_0$).

In addition, the following reproductive parameters were estimated: gross and net fecundity rates, mean daily offspring production, and mean age for gross and net fecundity. The population demographic parameters were net reproductive rate (R_0), intrinsic rate of increase (r) using Newton's method based on the formula $r_i = r_0 - f(r)/f'(r)$, finite rate of increase (λ), mean generation time (T), and doubling time (DT).

Data analysis

The experimental design was completely randomized with two treatments (hosts) and 30 replicates, considering each pair of parasitoids as an experimental unit. The data were tested for normality by means of Anderson-Darling test, and for homogeneity of vari-

ances with the Bartlett and Fligner-Policello tests. The pre-oviposition and reproductive periods were compared by means of t-student and Mann-Whitney test, respectively.

Sex ratio and percent parasitism were analysed using a generalized lineal model (GLM) with quasibinomial response, whereas fecundity (offspring per female) was a GLM with negative binomial response. The link-log function was used in each model and a likelihood ratio test was applied to test for the effect of the treatments. Survival curves for females and males were compared using the Log-rank test. A significance level of .05 was used for all statistical tests. All analyses were carried out using the statistical software R v4.0.5 (R Development Core Team 2021).

Results

Immatures developmental time and survival

The mean developmental time from egg to adult was 19 days for both host species. Survival of immatures was 68.37% in *A. ludens* and 57.5% in *A. obliqua*. These data were used to construct the life tables and estimation of demographic parameters.

Oviposition period, parasitism, and sex ratios

The onset of oviposition occurred from the first day of female adult life (first 24 h) for both cohorts. The average female matured on the third day, and it ranged from 1 to 11 days in *A. obliqua* and from 1 to 13 days in *A. ludens*; the pre-oviposition period did not show significant differences ($W = 368$, $p = .9506$) between species. Within the reproductive period, the cohort exposed to *A. obliqua* lasted on average ($\pm SD$) 13.5 ± 4.99 days with a range of 1 to 21 days, while the cohort exposed to *A. ludens* lasted 11.5 ± 6.11 days with a range of 1 to 22 days. The difference in the reproductive period of both treatments was not significant ($t(2) = -1.2899$, $p = .2028$).

The percentage of days in which females produced at least one offspring was 65.7% and 86.1% for *A. obliqua* and *A. ludens*, respectively. This means that the cohort parasitizing *A. ludens* larvae produced more offspring in a shorter time. Fecundity (offspring per female) was significantly higher in females from *A. ludens* ($\chi^2(1) = 15.551$, $p < .001$). The maximum number of offspring per female was 191 with a mean ($\pm SD$) of 91.83 ± 67.77 individuals per female. For those exposed to *A. obliqua* larvae, the maximum offspring per female was 149 with a mean of 82.33 ± 41.87 individuals (Fig. 1).

The cohort using *A. obliqua* larvae as a host reached its maximum reproductive peak between four and six days, and by day seven 1241 offspring (50.24%) had been produced. In the case of females that parasitized *A. ludens*, the reproductive peak occurred between five and seven days of age, and by day eight they had produced 54% (1507 individuals) of their total offspring (Fig. 2).

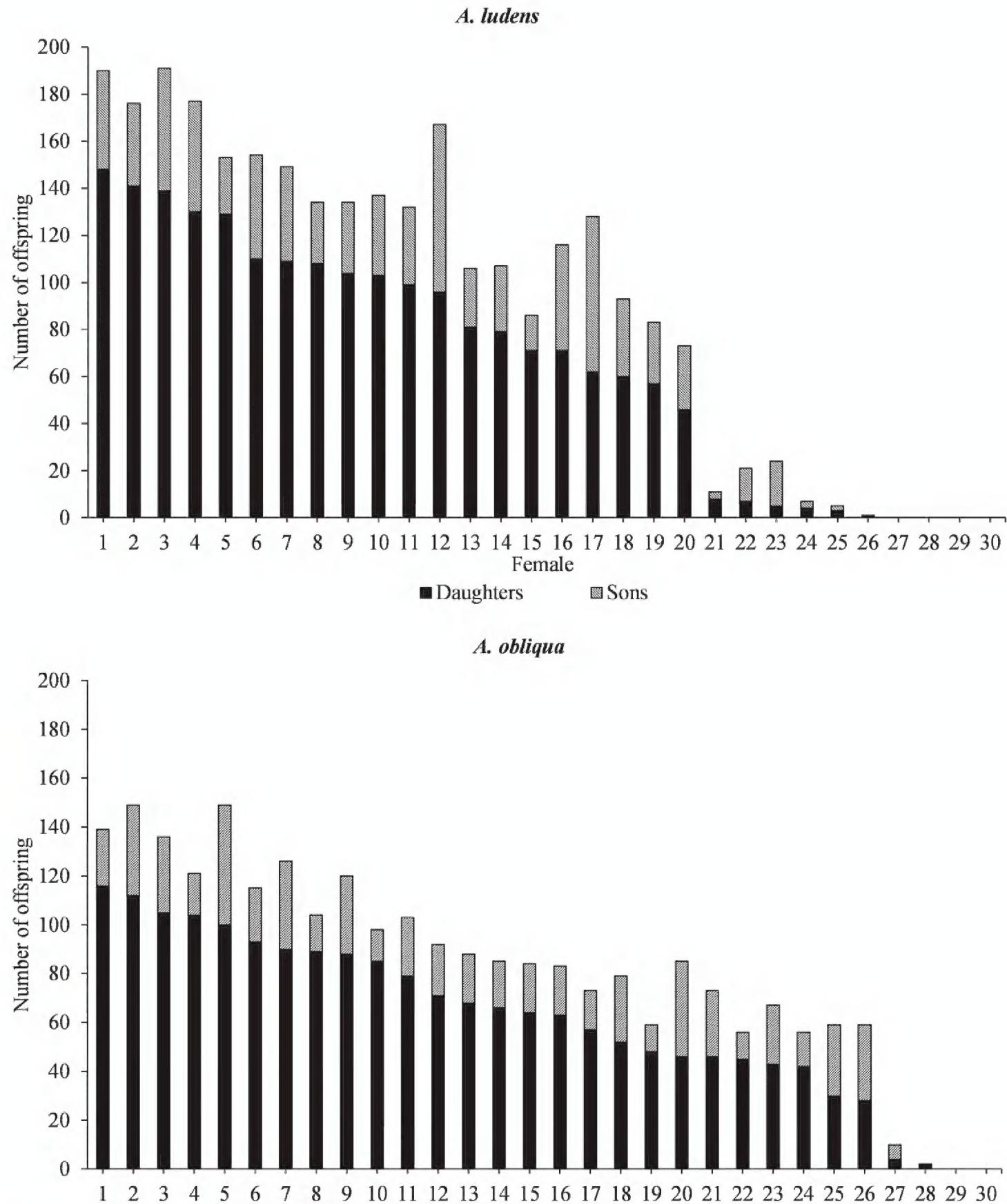


Figure 1. Total offspring and sex ratio produced by each female, in both cohorts studied.

Average percentage (\pm SD) of total parasitism was higher ($\chi^2(1) = 4.4137$, $p = .0357$) in *A. ludens* larvae ($16.72 \pm 11.56\%$), than in *A. obliqua* ($13.04 \pm 9.69\%$, Fig. 3). Offspring sex ratio was biased towards females (around 70%) ($\chi^2(1) = 0.98385$, $p = .3213$) and this was observed through the whole females life span in both species ($\chi^2(1) = 0.00014$, $p = .9904$). In *A. obliqua* a proportion (\pm SD) of 0.73 ± 0.13 females was observed. In *A. ludens* it was 0.69 ± 0.16 .

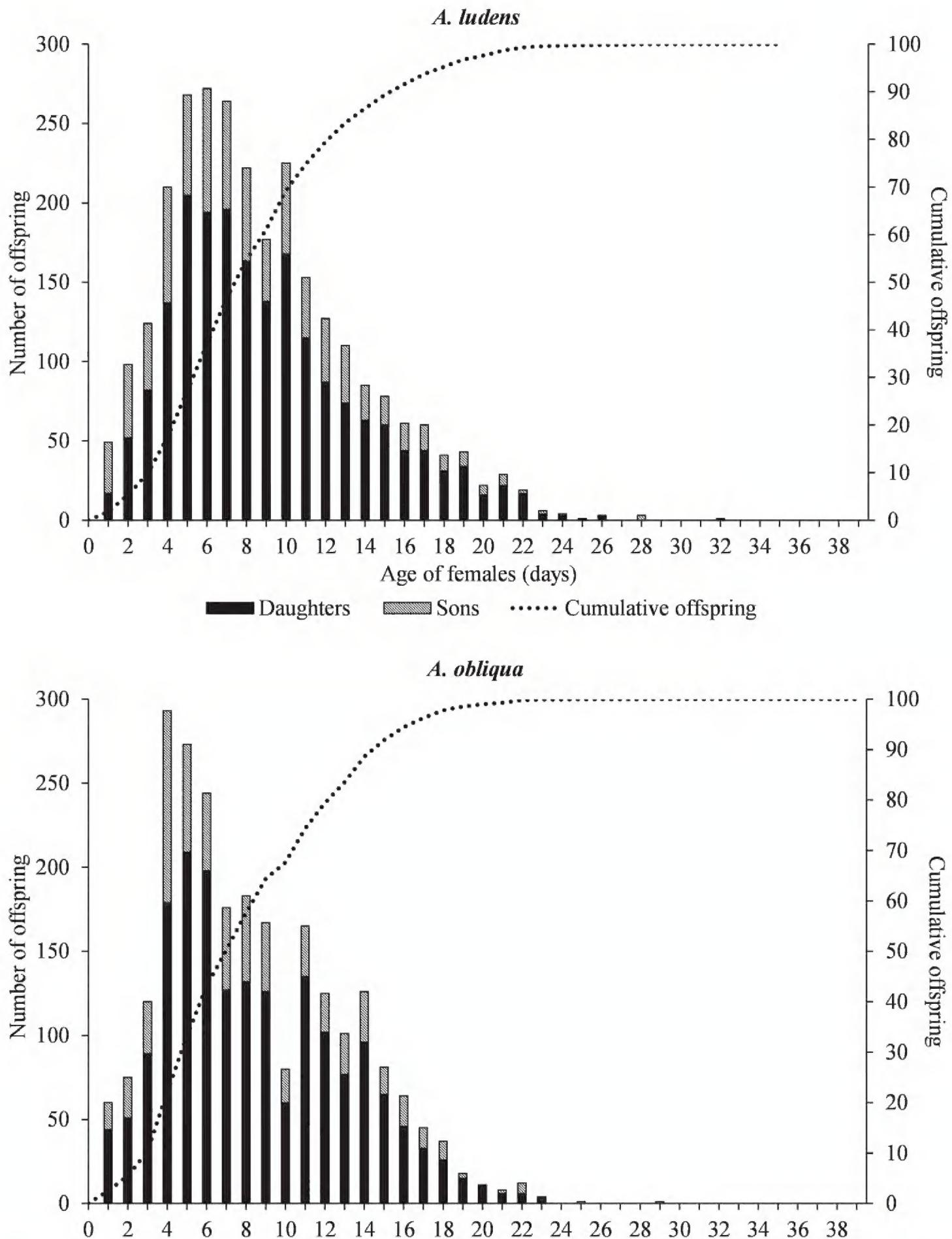


Figure 2. Daily offspring and sex ratio of *U. anastrephae* emerged from *A. obliqua* and *A. ludens* larvae as hosts and their respective cumulative frequency.

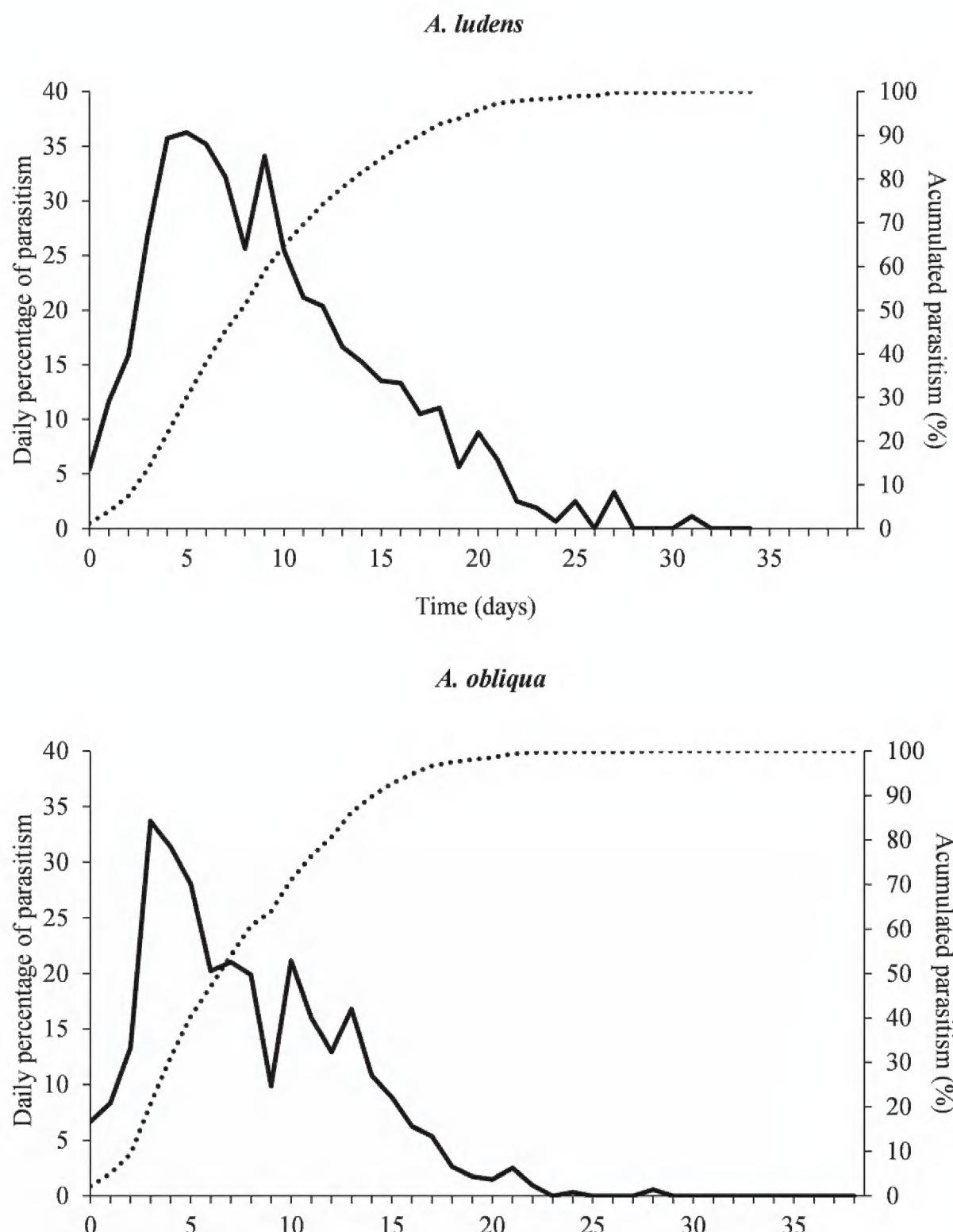


Figure 3. Daily percentage of parasitism of *U. anastrephae* in *A. obliqua* and *A. ludens* as hosts.

Survival, reproduction, and population demographic parameters

Female survival was different (Log-Rank $\chi^2 (1) = 4.6$, $p = .03$) between the two cohorts.

Females parasitizing *A. obliqua* larvae showed greater survival than those parasitizing *A. ludens* larvae with a mean longevity of 22.93 ± 8.37 (mean \pm SD) and 16.93 ± 9.67 days, respectively (Fig. 4). In both cohorts, males lived less than females, without statistically significant difference in their survival (Log-Rank $\chi^2 (1) = 0.82$, $p = .4$). Males in the cohort with *A. obliqua* had a mean longevity of 13.33 ± 7.59 days and 15.63 ± 7.22 days with *A. ludens*.

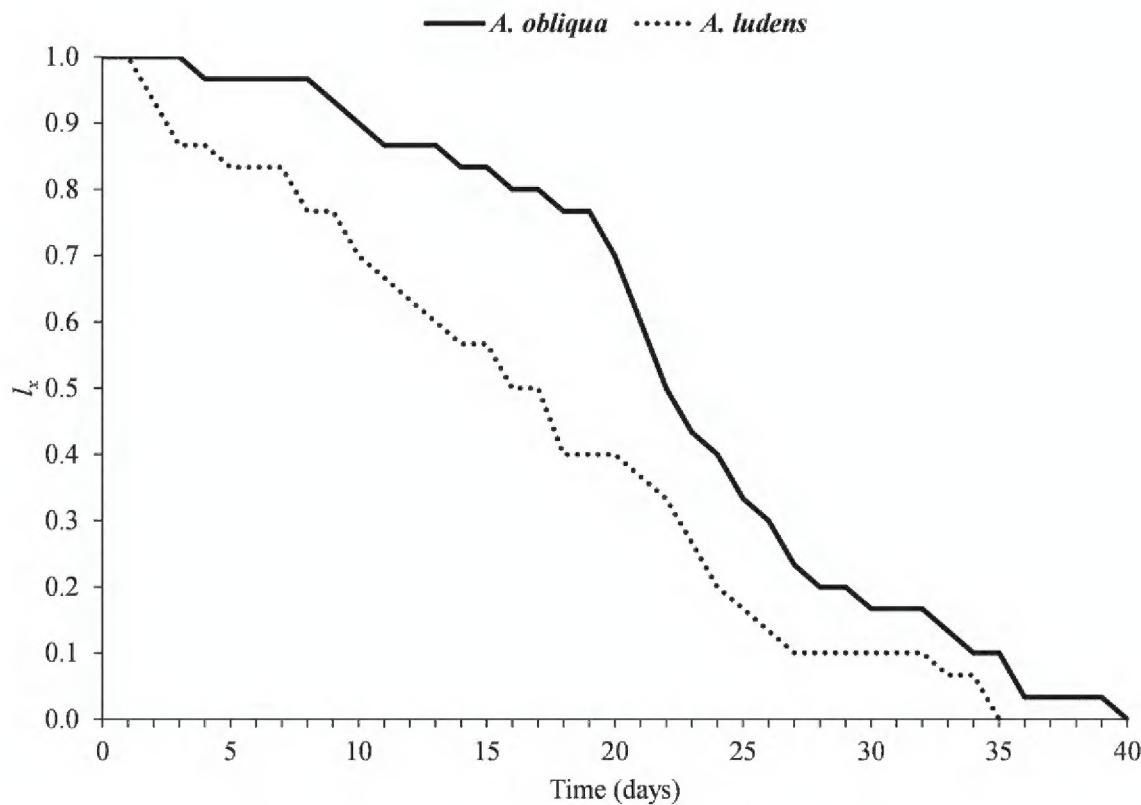


Figure 4. Survival curves of *U. anastrephae* females parasitizing larvae of *A. obliqua* and *A. ludens* as hosts for the respective offspring development.

Reproductive rates were greater for parasitoids using *A. ludens* larvae as hosts than those using *A. obliqua*. The trajectories of net fecundity for both cohorts are shown in Fig. 5. Table 1 shows the gross and net fecundity rates, the daily mean of offspring production and the mean age for gross and net fecundity for the two cohorts. Regarding the population demographic parameters (Table 2), while the net reproductive rate (R_0) was higher in *U. anastrephae* females that parasitized *A. ludens* larvae, all other population parameters were very similar for the two cohorts. The intrinsic rate of increase was similar (≈ 0.13) between the two cohorts.

Discussion

It was interesting to find that *U. anastrephae* could develop equally successfully in both hosts, one of them being its most frequent natural host (*A. obliqua*), and the other its host in the laboratory rearing colony (*A. ludens*). *Anastrepha ludens* has been reported as the natural host of *U. anastrephae* very rarely (Montoya et al. 2016). However, since most studies on natural parasitism of fruit fly parasitoids have generally been directed to the same fruits of specific interest (Aluja et al. 1990; López et al. 1999; García et al. 2020); it is possible that other fruits that have not been inspected are hosting *A. ludens* parasitized by *U. anastrephae*. Likewise, there may be confusion regarding the emergence of *U. anastrephae* from *A. obliqua* when it could also emerge from *A. ludens*, since parasitoids have been detected in mango, where both species of flies are present (Aluja et al. 1990). However, this assumption needs to be investigated.

Table 1. Reproductive parameters of *U. anastrephae* with larvae of *A. obliqua* and *A. ludens* as hosts.

Reproductive parameters	Host	
	<i>A. obliqua</i>	<i>A. ludens</i>
Gross fecundity rate	91.06	136.26
Net fecundity rate	47.50	62.61
Mean daily production	1.68	2.23
Mean age gross fecundity	28.90	30.37
Mean age net fecundity	28.41	28.84

Table 2. Population demographic parameters of *U. anastrephae* with larvae of *A. obliqua* and *A. ludens*.

Population parameters	Host	
	<i>A. obliqua</i>	<i>A. ludens</i>
Net reproductive rate (R_0)	35.31	44.80
Mean generation time (T)	27.88	28.30
Intrinsic rate of increase (r)	0.128	0.134
Finite rate of increase (λ)	1.14	1.14
Doubling time (DT)	5.42	5.16
Adult life expectancy (e_x)	22.4	16.4

The higher reproductive rates found when *A. ludens* larvae were the host, compared to *A. obliqua*, can be attributed to three factors: 1) the effect of host switch, 2) the quality of the host, and/or 3) the immunological response. It is known that host switching may adversely affect the fitness of parasitoid species during the very first generations in a new host, although in subsequent generations their performance can improve (Zenil et al. 2004; Jones et al. 2015; Poncio et al. 2016). When the parasitoid *D. longicaudata* was previously maintained on *A. fraterculus* larvae, the adults parasitized more on this host than when *Ceratitis capitata* larvae (Wiedemann, 1824) were offered as an alternative host (Ovruski et al. 2011; Rohr et al. 2019). Something similar was observed with *Fopius arisanus* (Sonan, 1932) reared on *C. capitata* larvae for 28 generations. When adults were exposed to *Anastrepha* species larvae, the percentage of adult emergence was lower than in those exposed to *C. capitata* larvae (Zenil et al. 2004).

The use of alternative (factitious) hosts for parasitoid rearing has been an important technique (Pluke and Leibee 2006). When parasitoid colonization with the native host is a difficult, or expensive process, the use of this factitious host becomes an option (Boycheva et al. 2019). As mentioned above, *U. anastrephae* colonization with *A. obliqua* as host was an ineffective process. The use of *A. ludens* larvae as factitious host represented a good option.

Regarding the immune response of *A. obliqua* to parasitoids, it has been reported that its larva possesses 5–6 types of haemocytes that generate a strong immune response (phagocytosis and production of reactive oxygen species) (Silva et al. 2002; Gómez-Alonso et al. 2022). The presence of these haemocytes resulted in the melanization and encapsulation of the first immature stages of parasitoids (Silva et al. 2002; Cancino et al. 2022), which has not been observed in *A. ludens* (Poncio et al. 2016; Cancino et al.

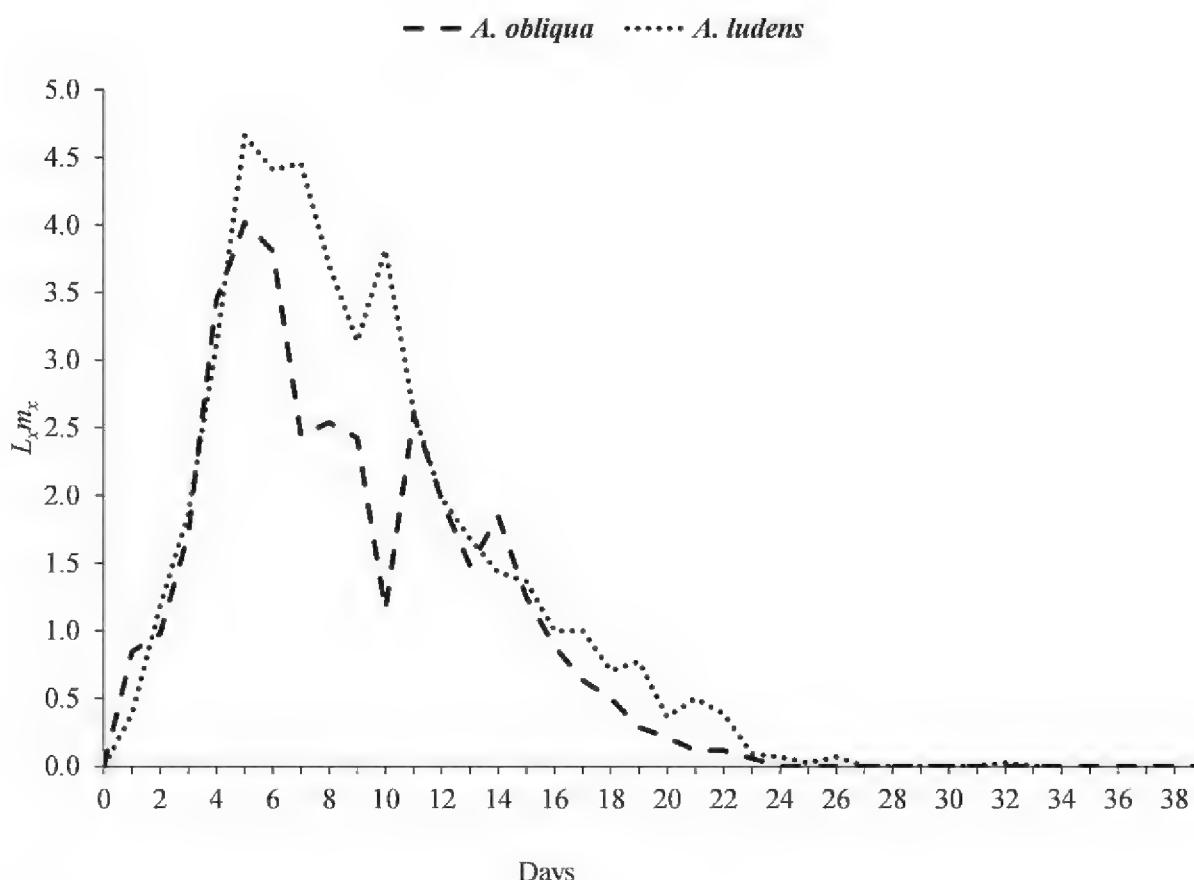


Figure 5. Daily results of net maternity ($L_x m_x$) of *U. anastrephae* with offspring daughters emerged from *A. obliqua* and *A. ludens*.

2020). This high immunity response of *A. obliqua* larva represents an important factor in increasing parasitoid mortality during development.

Host quality could be another factor. *Anastrepha ludens* larvae are larger in size than the *A. obliqua* ones. Under mass-rearing conditions, the mean pupal weight is 20 mg for *A. obliqua* and 24 mg for *A. ludens* (Orozco-Dávila et al. 2017). Usually, larger size hosts are preferred by parasitoids, showing an increase in their fecundity (Brodeur and Boivin 2004; Cohen et al. 2005; Gao et al. 2016). Another reason may be the better adaptation and more stability of *A. ludens* to mass rearing conditions. Compared with *A. obliqua*, it has been, easier to colonize and maintain under laboratory conditions (Orozco-Dávila et al. 2017; Aceituno-Medina et al. 2020).

The lower survival of the parasitoids exposed to *A. ludens* larvae can be explained by the cost of reproduction, the higher the fecundity, the lower the longevity. Since the net reproductive rate and the intrinsic rate of increase were higher for parasitoids reared on *A. ludens* than those reared on *A. obliqua* (Table 2), this trade-off can be considered convenient in terms of fitness.

The demographic parameters we found here were like those reported by Vargas et al (2002) with other larval-pupal braconid endoparasitoid reared on different hosts. For example, the intrinsic rate of increase for *D. longicaudata* and *Psyttalia incisi* (Silvestri, 1916) was $r = 0.12$ and 0.10 , respectively, both reared on *Bactrocera dorsalis* larvae (Hendell, 1912). This suggests that *U. anastrephae* has the potential to be used as a biocontrol agent, as it has growth rates like other parasitoid species that have been used for the control of fruit flies.

The intrinsic growth rate we found here with *A. ludens* as a host ($r = 0.134$) was 2-fold greater than that reported by Aluja et al. (2009) using the same host when they were colonizing this species for laboratory rearing ($r = 0.079$). This means that the *U. anastrephae* strain tested here has adapted to this alternative host species, and it can be used for mass production. The sex ratio is a fundamental aspect for biological control, since the females are the ones that attack the host and contribute to population growth. A female-biased sex ratio would be most desirable (Montoya et al. 2013; Nurkomar et al. 2021). Here we found that the sex ratio was female-biased, about 70% female ($\approx 3:1$) for both hosts used. This proportion coincides with that obtained by Poncio et al. (2018), with a percentage of 65% using *A. obliqua* larvae as hosts. This proportion is adequate for the purposes of augmentative biological control.

The reason why under natural conditions *U. anastrephae* is commonly associated to *A. obliqua* could be the size of the fruit species used by the fruit fly species (Hernández-Ortíz et al. 1994; López et al. 1999). *Utetes anastrephae* has a short ovipositor that might be strongly adapted to small fruits. In general, *A. obliqua* infest fruits that are smaller in size (*Spondias* spp., *Psidium guajava* L.) than those commonly infested by *A. ludens* (*Citrus* spp., *Casimiroa edulis* La Llave & Lex). Then, in large fruits the host larvae might be out of reach for *U. anastrephae*. Also, semiochemicals emitted by fruits infested by *A. obliqua* (usually small) can determine this preference (Aluja et al. 2013). Another possibility, derived from our results, will be to use *A. obliqua* as a host for several generations, expecting that reproductive and population parameters could increase. However, the greater difficulty and cost of producing *A. obliqua* should be considered.

This demographic analysis of *U. anastrephae* comparing two hosts indicates that *A. ludens* can be used as a suitable host for mass production, although releases of parasitoids be strategically targeted to control *A. obliqua*. Biological control of *A. obliqua* in non-commercial hosts could be a strategy to prevent the movement of populations from these hosts to fruit orchards (i.e., mango orchards), where fruits are grown for commercial purpose (Cancino et al. 2019b; Montoya et al. 2000). *Anastrepha obliqua* is a major pest of mango in the Americas and is highly desirable to have a biocontrol alternative to minimize its damage (Cancino et al. 2019b; Ruiz-Arce et al. 2019).

The information generated here can be useful for decision making on the use of native parasitoids in augmentative biological control and new proposals to complement or improve current strategies for managing *Anastrepha* fruit flies. It would be interesting to know the behaviour of *U. anastrephae* reared in *A. ludens* larvae, on host preference in the presence of these two host species studied here, both in the laboratory and under field conditions.

Conclusion

This study provides information about the potential use of the native parasitoid *U. anastrephae* in augmentative biocontrol programs against *A. obliqua* fruit flies. Our results show that both, *A. obliqua* and *A. ludens* larvae can be used as hosts for mass

rearing purposes. Although *A. ludens* is not a common natural host, it can be used as a factitious host, considering the higher fecundity rate observed and considering that *A. ludens* is easier to mass produce than *A. obliqua* (Orozco-Dávila et al. 2017).

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